LABORATORY REFERENCE DOCUMENT NO. 81-26

A Critique of BENTHOS

A simulation model by J. R. Albanese

by

[1]Wendell Hahm and [2]Thomas M. Leschine

☑ Approved for Distribution

☐ Distribution to F/NWC, F/SWC, F/SEC, F/NWR1, & F/NEC (Technical Writer-Editor)

Signature M. D Grosslein

Date 9 Nov 1981

[1]National Marine Fisheries Service
Northeast Fisheries Center
Woods Hole Laboratory
Woods Hole, Massachusetts 02543

[2]Marine Policy Program
Woods Hole Oceanographic Institution
Woods Hole, Massachusetts 02543

October 1981

INTRODUCTION

BENTHOS is the product of J.R. Albanese (1979) of the Center for Ecological Modeling (CEM), at Rensselaer Polytechnic Institute. The Center for Ecological Modeling, founded in 1977, grew out of work on the International Biological Program (IBP) lake ecosystem studies. The Center has concentrated on modeling lakes and aquatic ecosystems for research and management applications. The Albanese model shares many of the methods used in CEM's predecessor lake models [CLEAN (Park et al., 1974) and CLEANER (Park, Scavia, and Clesceni, 1974)]. The major difference is that BENTHOS is intended to simulate a marine rather than an aquatic system. BENTHOS is designed to use the same utility subroutines as MS.CLEANER (Park et al., 1979), one of the models of this series.

This review was prepared at the request of investigators at the University of Rhode Island's Graduate School of Oceanography who are involved with MERL (The Marine Ecosystem Research Laboratory), to help them assess the possible utility of BENTHOS for on-going MERL research. MERL is a large scale microcosm experimental system located at URI's Narragansett Campus adjacent to Narragansett Bay. In operation since 1976, the system consists of 14 cylindrical tanks, each 1.8 m in diameter and 5.5 m in height, and holding about 13 m^3 of Narragansett Bay water over 1.1 tons of Bay sediment. The water is circulated via a pulsed flow chemostat-like pumping system. A mechanical plunger is used to simulate natural mixing in the tanks and heat exchangers keep them within ± 3°C of Bay temperatures.

These microcosms have been used for a variety of experiments. Studies have been both long and short term; by using different tanks to represent perturbed and control states of the system, MERL experimenters have been able to analyze the Bay's response to both natural events and a number of man-induced stresses. A long term study of the effects of chronic low level oil pollution has been conducted, as have a number of studies of the effects of various other pollutants added to the water column in the tanks. Other studies have focused on the effects of pollutants contained in Bay sediments, and ^{14}C labeled tracers have been used to measure the transfers of carbon among various components of the Bay ecosystem.

Other tracer studies have followed the time course of volatile organics (such as freon) and radioactive isotopes (such as plutonium) through the water column and benthos. Comparative microcosms set up with and without the benthos have been used to assess the role of the benthos in the system. Similar experiment designs involving nutrient enrichments and environmental gradients have been carried out. The "mixing experiment" attempted to separate out the effects of turbulence on the Bay's lower trophic levels by comparing tanks run with and without the mixing action of the plunger. Figure 1 shows a MERL microcosm in schematic representation and indicates the kinds of data that are collected in MERL experiments. Oviatt et al. (1980), Pilson et al. (1980), and Elmgren and Frithsen (1981) give a more detailed accounting of the work that has gone on at the laboratory.

This review is written in three parts. The first section describes the structure of the BENTHOS model. The second contains our critique of it. The third and final section assesses the model's utility with respect to the on-going experimental studies being conducted with the MERL system, which BENTHOS is intended to simulate. We find the usefulness of BENTHOS to be limited; we outline reasons why we believe this to be so.

BENTHOS is a generalized model, reminiscent of the large scale IBP models. Difficulties can arise, however, when such general models are, after the fact, applied to specific systems. Numerous authors have argued both the conceptual problems of building large ecosystem models and the more practical problems of interpreting and explaining the output of such models in terms of the behavior of the systems they represent. See, for example, Watt (1975), Caswell (1975) and Pielou (1981). We find in the Albanese model difficulties similar to some of those described in general terms by these and other authors.

A REVIEW OF BENTHOS

I. The Form and Complexity of the Model.

BENTHOS is a detailed simulation model of a marine macrobenthic ecosystem. The model is intended to represent the Narragansett Bay ecosystem in the sense that it is calibrated with data from MERL Microcosm Tank One (the control tank) and verified via comparison with field measurements made in Narragansett Bay. BENTHOS takes the form of 25 simultaneous differential equations which describe the rates of change of each of the model's 25 state variables. The first twelve equations represent a metabolic mass balance of four macrobenthic niches: omnivores, suspension feeders, selective deposit feeders, and indiscriminate deposits feeders. Any change in biomass dB/dt is calculated as the difference between consumption and i) metabolic demands (i.e. respiration + elimination + excretion); ii) reproduction, and iii) mortality (natural, trophic, or fishing).

The next eight equations describe the pools of dissolved and particulate organic matter in the water column and the sediments. Each type of organic matter is further classified as being either labile or refractory. Particulate organic matter (POM) is derived through defecation or natural mortality of organisms. Sedimentary POM is advected into water column POM by currents. POM is in turn slowly transformed into dissolved organic matter (DOM). The dissolved organic pool gains through excretion by organisms and external inputs, such as by tides. DOM and POM in the water column are advected through tidal processes. DOM and POM in the sediments are also lost through burial and diffusion.

The last five equations concern inorganic sediments. One of these represents the sand and silt size suspended particles, while two other equations represent the settling of particles to the sediments. Another pair of equations is used to represent oxygen levels in the water column and interstitial waters.

There are three levels of equations in this model. The first is the system of differential equations described above. The second type of equations are termed "process equations" and represent other empirically observed processes which are not explicitly modeled, such as sediment erosion, sedimentation and remineralization. Each such process equation is calculated by a subroutine and each may be a function of state variables, driving variables, or various model parameters. Both linear and non-linear equations are used and more than a dozen such equations are described. The third type of equations describe what are termed "correction-factor" functions. These are terms which modify calculated exchanges between model compartments on the basis of oxygen or temperature limitation, crowding among organisms, or other similar factors.

II. Comments on the Model.

It is difficult to assess a model simply on the basis of its equations and a few line graphs. We did not run the model (which is available on a

9 track tape from CEM). Quite a bit of bias can be woven into the computer algorithms used in such a model. These comments are therefore general impressions based on model form and structure and on our analysis of the suitability of the model to the goals and audience for which it is intended. Going from the general to the specific, they can be put into three categories: i) the approach; ii) the system, and iii) the equations.

A. The Approach.

Ecological models, like essays, are most effective when written for a specific audience. On one extreme, black box forecasting models concentrate on the statistical relationships between the experimentally measured inputs and outputs of a specific process. On the other extreme are general "heuristic" or analytical models based on a mosaic of hypothetical relationships. The aim of a forecasting model is to predict, with a specified accuracy, the outcome of a process, given specified input conditions. The aim of a heuristic model may be to demonstrate the probable mechanisms of processes within a system. In terms of model development it is possible to weave many forecasting models as submodels into a more generalized model. The reverse, going from a general model to a specific model, is not as plausible.

Nevertheless, in practice complex models like BENTHOS often combine elements of both approaches. Pielou (1981) uses the term 'investigation' to distinguish the first approach, which she describes as seeking empirical answers to single clearcut questions, from modeling per se. She argues that such statistically based investigations are not generally suitable to providing ecological explanations of the type mechanistic models are designed to give. Caswell (1975) argues similarly that validation of a predictive model by the successful reproduction of observed behavior in the system being modeled (through the generation of test statistics) is not tantamount to validating the ecological theory embodied in the model's construction. The same statistically significant correlations can follow from a variety of ecological explanations (Pielou, 1981) and a model which successfully reproduces observed data can still fail on theoretical grounds (Caswell 1975). Caswell (1975) also argues that modeling projects which mix the goals of achieving both predictive and theoretical validity run the risk of generating only confusion, noting that many of the IBP models do explicitly mix these two purposes. This thread of mixed purposes is certainly to be found in BENTHOS, where the comparison of model predictions to observed values of the corresponding state variables in Narragansett Bay is presented as a validation of the model as an accurate representation of marine benthic ecosystem processes (Table II and Figs. 41-47).

BENTHOS is a generalized model of macrobenthic interactions with organic matter, sediments and physical forcings. Problems do seem to occur when this generalized model is applied to a specific ecosystem. The practice of fitting general models to a specific ecosystem presumes the understanding of a basic structure shared by different systems. If the intent of the modeler is to describe the dynamics of the MERL system, the best approach might be to base the model on specific empirical (forecasting) submodels derived at MERL. This was not done. The practical problems of converting a general model for use on a specific ecosystem study are twofold: data and utility.

i. Data. The substance of a model is as good as its data base. Of the 297 system parameter values listed in Appendix II only 25 can be traced to data derived from MERL. One of these was the depth of the microcosm tank and 20 are "fitting" constants used to fit the output to a one-year cycle of observed macrobenthic levels. Four are estimates of particle cohesiveness.

An additional eleven were based on Narragansett Bay studies. The balance of coefficients were from both the aquatic and marine literature.

ii. Utility. This sparse use of what is in fact a very large data base is not appropriate for a model constructed to be used as an integrator of activities and observations made in an actual experimental ecosystem. A household model should be lean and data oriented to test what is being actually observed. There is enough noise in the experimental data set. Adding details which are unmonitored in the laboratory can only produce confusion when an investigator tries to use the model to help evaluate the causes and responses being studied.

One measure of a model's utility is how well it can be verified. A model can be accepted on the grounds that either its outputs are biologically sound or that it produces reasonable facsimiles of observed data. BENTHOS is verified in the latter sense. Since there are serious questions about how the model was fitted to the observed data (See Section B. The System), the fit the model makes to the observed population levels is somewhat surprising. One is more inclined to question how such accuracy was achieved than to accept such results as proof of the model's success at capturing the essence of the underlying mechanisms.

BENTHOS is a model constrained by fitting coefficients to conform with a single year's data. The problems are twofold. First the model aims at point estimates of biomass not taking the attendant variability into consideration. Second, the model is "driven" by external forcings (POM and DOM inputs, temperatures, salinity, etc.) to replicate curves of biomass levels over time on a yearly basis. BENTHOS' three-year simulations (Figures 48 and 49) predict population cycles which do not change from year to year except in magnitude (like: $y = e^{-kt} * \sin t$).

The object of a simulation model should be to demonstrate ecological mechanisms, and in so doing, mimic nature. BENTHOS seems to mimic nature without really simulating the underlying mechanisms.

B. The System.

Albanese sought to model the relationship of the macrobenthos to inputs of organic and inorganic matter and to other physical forces. There are two difficulties with the actual system derived. First, it is incomplete. Second, the form of the process equations decouples the system.

In this model dissolved and particulate organic matter are utilized by just the macrobenthos. This overlooks the significant metabolic activity of the meio- and microfauna, which are not included in the model. In fine sediments, while the biomass relationships of macro:meio:micro fauna might be 190:1.5:1, the ranking in terms of relative metabolic activity is roughly 3.7:1:1.4 (T. Fenchel, 1969).

BENTHOS appears to be driven by the observed annual temperature cycles. The temperature optima for the omnivores, suspension feeders, and selective and indiscriminate deposit feeders are set at 20, 5, 9, and 18 degrees Centigrade, respectively (Appendix II). Examination of the input temperature curve (Figure 30) reveals that the system reaches 20°C on about day 239. This roughly coincides with the omnivores' biomass density peak. The system reaches 5°C on day 70. This also coincides with the biomass density peak of the suspension feeders in Figure 33. Similarly, the tanks reach 9°C on days 112 and 348. Again, the selective feeders peak on about days 112 and 348 (Figure 34). Finally, the deposit feeders' temperature optimum is obtained on day 238 and the peak biomass density is reached on about the same day. Because the temperature cycle is clock-like and because the population is a slave to temperature, the populations will oscillate regularly on a yearly basis. This is borne out in the three-year simulation runs (Figures 48-49). The peaks can be moved to fit any data set simply by changing the optimum temperature coefficients. The heights of the peaks are governed by the initial population density and the carrying capacities set by the user. Temperature and not population dynamics appears to govern BENTHOS. In like manner, the model lacks the "biology" behind the production and conversion of particulate organic matter to dissolved organic matter. The conversion of POM to DOM is treated as a Michaelis-Menton type function of POM (Equation 16.0).

The ease of fitting macrobenthos biomass outputs to observed biomass levels results from the decoupled nature of the system. Scanning the interaction matrix of Appendix II for the MERL tank simulation reveals that there are no predator-prey interactions among the macrobenthic organisms. All feed on inputs of organic matter and not each other. Each population operates independently of its neighbors. This makes it unnecessary to model intercompartmental interactions. Unitless correction-factor functions like "crowds," (Equation 22.1) which lack biological reality, are used to adjust the factors used to compute biomass as a function of time.

C. The Equations.

i. One of the temptations of large scale modeling is to incorporate immediately all the complexity that is imaginable. Such models quickly exceed the available data. Increasing the complexity of a model often decreases its predictive powers. For one thing, the profusion of terms and equations makes it difficult to pinpoint the critical determinants of a model's observed behavior. A second problem arises with the estimation of critical parameters.

An example of over-parameterization is to be found in the details of the resuspension function (Equation 8.3), one of the model's empirical process equations:

$$\text{ERODE} = \text{B(J)*KERD*exp}\left(\frac{\text{CRNT*SHAPE*RADIUS}^2\text{*VIS*CRDIS}}{\text{g*(DEN-DENS)*RADIUS}^3\text{*SHAPE}} \quad -1\right)$$

The use of such a formula in a model like BENTHOS can be criticized on several grounds. While such theoretical formulations (based on Stokes Law for low Reynolds number flow) are familiar to fluid dynamicists, they are unfamiliar to most ecologists, who generally don't include the measurements required to parameterize such a function as part of experimental programs designed to measure biological processes. More to the point, measurements of sediment particle radii, shapes and cohesiveness have not been made in the MERL project, either in the microcosms or in Narragansett Bay. The values of these parameters actually used in model runs are described only as "estimated" (Appendix II) with no reference other than to a basic text in mineralology.

From the other point of view, experimentally-oriented fluid dynamicists have long been frustrated by the difficulty of fitting such theoretical models to data. The measurements necessary to fit models such as that above are difficult to make and characteristically show high variances about their means. Other factors not included in the Albanese formulation, such as the relationship between bedload and suspended load in flow and other boundary layer properties, often prove critical in discriminating among candidate models (Graf, 1971). The problem is particularly difficult in unenclosed waters, like Narragansett Bay. In short, the uncritical use of Equation 8.3

in this situation is naive from the standpoint of the fluid dynamicist. The detail required for such a formula to be used is, for all practical purposes, unobtainable for the systems BENTHOS is designed to represent. It would probably have been more desirable to use a simpler and more familiar (to ecologists) form of the resuspension equation, to allay fears that complex and untestable hypotheses about the behavior of subsystems of second order importance may be governing the behavior of the model's primary components.

ii. In addition to the detail of the process equations, there seems to be a problem with the use of correction factors. Processes such as respiration and ingestion are modified by limiting factors lim_i in the form $\text{FACTOR} = A*[\prod_{i=1}^{n}\text{lim}_i]$.
For example, Ingestion = C*[TEMP*02COR*BEHAVE*POPUL*CROWDS] (Equation 20.7). Similarly, Respiration = (RMAX*B(J)+CORES)*BEHAVE*RESTEMP*POPUL*CROWDS. There are two potential problems. First, the same correction terms are being used on different processes, suggesting that multiple processes are affected the same way by environmental cues (temperature, crowding, etc.). The second problem stems from the multiplicative condensation of correction factors. The product is invariably low, resulting in overinhibition of the system (i.e., if $\text{lim}_1 = \text{lim}_2 = \ldots = \text{lim}_5 = .9$, $\prod_{i=1}^{5}\text{lim}_i = .59$).

III. Modeling and MERL.

The MERL facility with its replicated large scale microcosms and extensive analytical facilities is producing a detailed time series of biological and nutrient data. The data accumulating from the various experimental studies are especially conducive to modeling efforts. The Narragansett Bay Model (Nixon and Kremer, 1977) has been adapted to simulate a microcosm recently by Kremer (pers. comm.). Several sediment models of isotope and metal distributions have been developed based on radioactive tracers (MERL, 1980). In addition, an empirical simulation and flow analysis model (MERLIN) based on the time series data sets is presently under development to investigate the recycling and nutrient flow dynamics within the microcosms.

What problems of overall system structure and function do MERL investigators find most interesting? Fish predation may have a significant impact on benthic populations in Narragansett Bay. Possibly because fish are excluded from the MERL tanks, large invertebrate predators, such as crabs, increased in abundance to the point where they significantly over-cropped the benthos during early MERL experiments. The density of these predators is now controlled by trapping. This observation suggests that MERL could be used together with modeling to investigate the effects of fish predation in the Bay.

Organic matter inputs to bottom sediments may be at least as important as predation in determining benthic populations. The "mixing" experiment revealed that continuous mixing of the water column decreased zooplankton populations and increased productivity, presumably making increased organic matter available to the bottom community. In a 'no mixing' control tank zooplankton populations increased while bottom productivity declined slightly. Larval input to the tanks from the bay also appears to have a strong though lesser effect than the above two processes on benthic biomass.

An important goal of MERL investigators is to determine the overall carbon flow structure of the MERL microcosms. A useful approach to modeling might thus focus on total population biomass rather than the population densities modeled by Albanese. Though one can expect densities to track temperatures to a certain extent, population models which do so are generally more life history-dominated than the Albanese model. Process oriented models like BENTHOS would appear to be more suitable to the investigation of process-related questions than to questions concerning biomass distributions. A more modest goal of such modeling could be to estimate total annual compartmental fluxes directly, or to determine the variables most sensitive to changes in flux rates. A model truly capable of simulating benthic organism densities in terms of organismic and community responses to system inputs would in fact be of great value to studies of the resuspension question discussed above. The bioturbation of sediments by benthic organisms is thought to play a significant role in determining resuspension rates in the MERL tanks.

The models of most use to experimentally oriented ecologists are no doubt those which evolve from programs of mutually supportive model building and experimentation. Such programs are sadly all too rare, with the situation described here more the rule. The Albanese model was not built in close collaboration with MERL investigators. It is therefore not surprising that it is unsuitable for dealing with the questions they currently find to be of greatest interest. BENTHOS does not appear to have been constructed to test any particular hypothesis about the marine systems in MERL, Narragansett Bay, or any other ecosystem.

It is too much to expect such a model to be of real predictive value for MERL experiments or Narragansett Bay population studies. The fact that BENTHOS fits some of the data may produce little more than puzzlement in investigators who either don't understand or doubt the importance of many of the processes it represents. On the other hand, the model, as presented in CEM Report 6, is logical and systematic in its consideration of the important processes which seem to govern marine ecosystems. It thus would seem to have great potential value as a demonstration model useful for explaining the principles of model building or of marine ecosystem dynamics. As such, the use of BENTHOS as a classroom tool should be considered by investigators at MERL.

In its completed form BENTHOS appears to fall victim to a confusion of the not necessarily complementary goals of reproducing observed data with reasonable accuracy on the one hand and demonstrating an ecosystem's underlying mechanisms on the other. As a demonstration model, the parts of BENTHOS may ultimately prove more useful than the whole. Many of its submodules appear potentially applicable to elucidating the contributions discrete processes make to ecosystem function, given appropriate (and explicit) sets of assumptions about the state of the rest of the system. The process equation for ERODE discussed above, for example, could be usefully used to illustrate the problems of estimating resuspension in shallow marine environments as well as to show how important a role this understudied process potentially has in contributing to marine productivity.

References

Albanese, J. R. 1979. A simulation model for coastal zoobenthic ecosystems. Rensselaer Polytechnic Institute, Center for Ecological Modeling. Troy, New York. CEM Rept. 6, 46 pp.

Caswell, H. 1976. The validation problem. In Systems Analysis and Simulation in Ecology, B.C. Patten, ed., Vol. IV: 313-325.

Elmgren, R. and J.B. Frithsen. In press. The use of experimental ecosystems for evaluating the environmental impact of pollutants: A comparison of an oil spill in the Baltic Sea and two long-term, low-level oil addition experiments in microcosms. In G. Grice and M.R. Reeve, eds., Marine Mesocosms: Biological and Chemical Research in Experimental Ecosystems. Springer-Verlag, New York.

Fenchel, T. 1969. Ecology of the marine microbenthos. Ophelia 6: 1-182.

MERL 1980. Report for year II of EPA Grant #806072020. The Marine Ecosystems Research Laboratory, 1980. Environmental Research Laboratory, Narragansett, R.I.

Nixon, S.W. and J.N. Kremer. 1977. Narragnasett Bay - The Development of a composite simulation model for a New England estuary. In C.A.S. Hall and J.W. Day, Jr., eds., Ecosystem Modeling in Theory and Practice: An Introduction with Case Histories. John Wiley, New York. pp. 621-673.

Oviatt, C. A., H. Walker and M. E. Pilson. 1980. An exploratory analysis of ecosystem behavior using multivariate techniques. Marine Ecology 2: 179-191.

Park, R. A., C. Desormeau Collins, D. Leung, C. Boylen, J. Albanese, P. deCaprariis and H. Forstner. 1979. The aquatic ecosystem model MS.CLEANER. Proc. First International Conference on State of the Art of Ecological Modelling, Copenhagen.

Park, R.A., R.V. O'Neill, J.A. Bloomfield, H.H. Shugart, Jr., R.S. Booth, R. A. Goldstein, J.B. Mankin, J.F. Koonce, D. Scavia, M.S. Adams, L.S. Clesceri, E.M. Colon, E.H. Dettmann, J.A. Hoopes, D.D. Huff, S. Katz, J.F. Kitchell, R.C. Kohberger, E.J. LaRow, D.C. McNaught, J.L. Peterson, J.E. Titus, P.R. Weiler, J.W. Wilkinson, and C.S. Zahorchak. 1974. CLEAN: A generalized model for simulating lake ecosystems. Simulation 23: 33-50.

Park, R.A., D. Scavia, and L.S. Clesceri. 1975. CLEANER: The Lake George model. In C.S. Russell (ed.), Ecological Modeling in a Resource Management Framework. Resources for the Future, Inc., Washington, D.C. pp. 49-82.

Pielou, E.C. 1981. The usefulness of ecological models: A stock taking. Quarterly Review of Biology 56: 17-31.

Pilson, M.E.Q., C.A. Oviatt and S.W. Nixon. 1980. Annual nutrient cycles in a marine microcosm. In J.P. Giesy, ed., Microcosms in Ecological Research, D.O.E. Symposium series, Augusta, GA. Nov. 8-10, 1978.

Watt, K.E.F. 1975. Critique and comparison of biomass ecosystem modeling. In Systems Analysis and Simulation in Ecology, B.C. Patten, ed., Vol. III: 139-152.

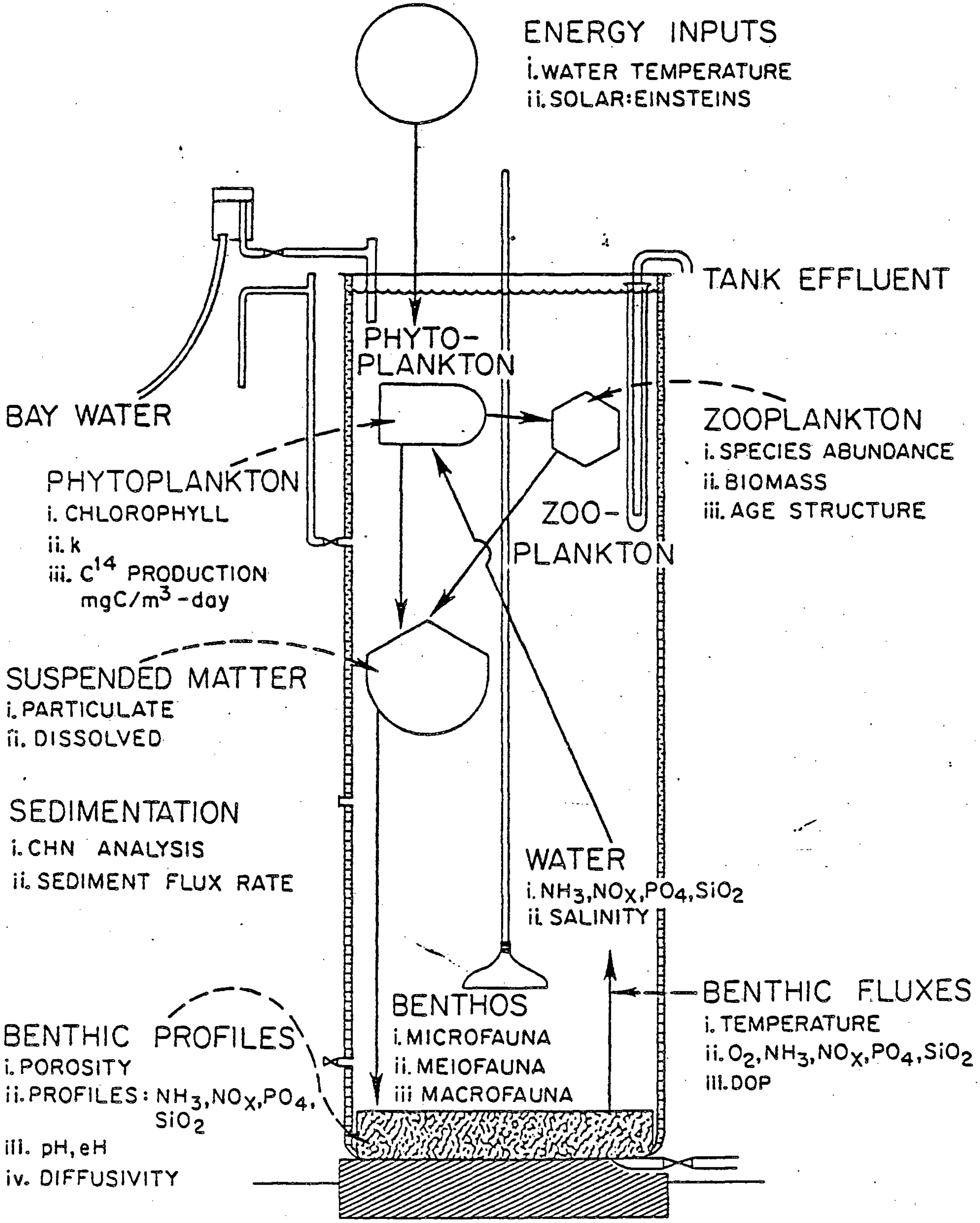
Acknowledgment

Thomas Leschine's work on this project was supported with funds from the Pew Memorial Trust and the Department of Commerce, NOAA Office of Sea Grant under Grant #NA80-AA-D-00077 (E/L-1).

Figure Legend

Figure 1. A schematic view of a MERL microcosm tank, with data collected in MERL studies indicated.

Figure 1.


ENERGY INPUTS
i. WATER TEMPERATURE
ii. SOLAR: EINSTEINS
TANK EFFLUENT
PHYTO-PLANKTON
BAY WATER
ZOOPLANKTON
i. SPECIES ABUNDANCE
ii. BIOMASS
iii. AGE STRUCTURE
PHYTOPLANKTON
i. CHLOROPHYLL
ii. k
iii. C^{14} PRODUCTION mgC/m^3-day
ZOO-PLANKTON
SUSPENDED MATTER
i. PARTICULATE
ii. DISSOLVED
SEDIMENTATION
i. CHN ANALYSIS
ii. SEDIMENT FLUX RATE
WATER
i. NH_3, NO_X, PO_4, SiO_2
ii. SALINITY
BENTHOS
i. MICROFAUNA
ii. MEIOFAUNA
iii MACROFAUNA
BENTHIC FLUXES
i. TEMPERATURE
ii. O_2, NH_3, NO_X, PO_4, SiO_2
iii. DOP
BENTHIC PROFILES
i. POROSITY
ii. PROFILES: NH_3, NO_X, PO_4, SiO_2
iii. pH, eH
iv. DIFFUSIVITY